RHODORA, Vol. 94, No. 880, pp. 362–370, 1992

CHROMOSOMES OF MEXICAN *SEDUM* VI. SECTION SEDASTRUM

CHARLES H. UHL

ABSTRACT

The four species of Section Sedastrum appear to comprise a natural group, but studies of 92 collections show three different basic chromosome numbers: $n = 20$ in *Sedum ebracteatum* and *S. hemsleyanum*, $n = 25$ in *S. hintonii*, and $n = 31$ in *S. glabrum*. The first two species are very similar and possibly should be treated as the same. Most plants of these two species are polyploids, up to $n =$ ca. 140. Many of the high polyploids are irregular at meiosis and probably reduced in sexual fertility. No clues are evident that suggest how these different basic numbers evolved.

Key Words: Crassulaceae, *Sedum*, chromosome numbers, Mexico

INTRODUCTION

This paper completes the reports on the chromosomes of the 100 or so species of *Sedum* that are native to Mexico and adjacent areas of the United States and Central America. Earlier papers (Uhl, 1976, 1978, 1980, 1983, and 1985) reported the chromosomes of 94 species and three probable hybrids that have been named as species. Methods and acknowledgements were given in Uhl (1976). Voucher specimens are in the Bailey Hortorium of Cornell University.

Rose (1905) described *Sedastrum* as a genus with clusters of dense, sessile rosettes of thick leaves and thick rootstocks. The inflorescence is an erect panicle about 30 cm high, bearing whitish flowers and dying to the base after flowering. The carpels have a distinctive basal concavity above the nectar scale. In some populations leaves and stems are streaked with red or purple, as in *Sedastrum rubricaule* Rose. More recent practice (e.g., Berger, 1930; Clausen, 1943, 1981) reduced the group to a section or subgenus of *Sedum*.

Rose (1905) recognized seven species that are distinguished from each other primarily by small differences in the shape and hairiness of the leaves. Generally following Clausen (1959, 1981), the eleven binomials that have been proposed for the species of Section Sedastrum are here reduced to four, and two of these intergrade substantially and perhaps should be combined. Three basic chromosome numbers are found, different in each of the three more easily separated groups.

The appendix lists the species alphabetically, and the collections are listed roughly from north to south, then from east to west.

SPECIES

Sedum ebracteatum DC

Sedum ebracteatum was the first species of Section Sedastrum to be described. DeCandolle (1828) based his description entirely on a drawing by Mocino, without ever having seen a plant, living or pressed, and he did not know the locality of its origin in Mexico. Clausen (1959) reduced five species, *S. barrancae* M. E. Jones, *S. chapalense* S. Watson, *S. cordifolium* Sesse and Mocino, *S. incertum* Hemsley and *Sedastrum rubricaule* Rose, to synonymy under *S. ebracteatum,* and later (Clausen, 1981) he added *Sedastrum pachucense* C. H. Thompson here—earlier he had placed it under *S. hemsleyanum.*

Leaves of *Sedum ebracteatum* are generally puberulent, but some plants resemble *S. glabrum* in the absence of hairs. However, the two differ significantly in their chromosomes, with basic numbers of 20 in *S. ebracteatum* and 31 in *S. glabrum,* and it seems best to keep them separate. Several more or less glabrous plants from within the range of *S. ebracteatum* that were once tentatively identified as *S. glabrum* had chromosome numbers based on 20 and were reassigned to *S. ebracteatum* for that reason.

Both *Sedum ebracteatum* and *S. hemsleyanum,* are relatively common, widely distributed and a bit variable in their morphology, and some collections are more or less intermediate between them. Clausen (1959) distinguished them chiefly by the broader leaves on the floriferous branches of *S. ebracteatum,* but this character is not completely consistent. Also, leaves and stems of *S. ebracteatum* are generally a bit less hairy than those of *S. hemsleyanum,* and it has a more northerly distribution, ranging from southern Tamaulipas, Coahuila and Durango south to the trans-Mexican volcanic belt. *S. hemsleyanum* extends from the volcanic belt southeastward into Central America, with possibly some overlap in distribution.

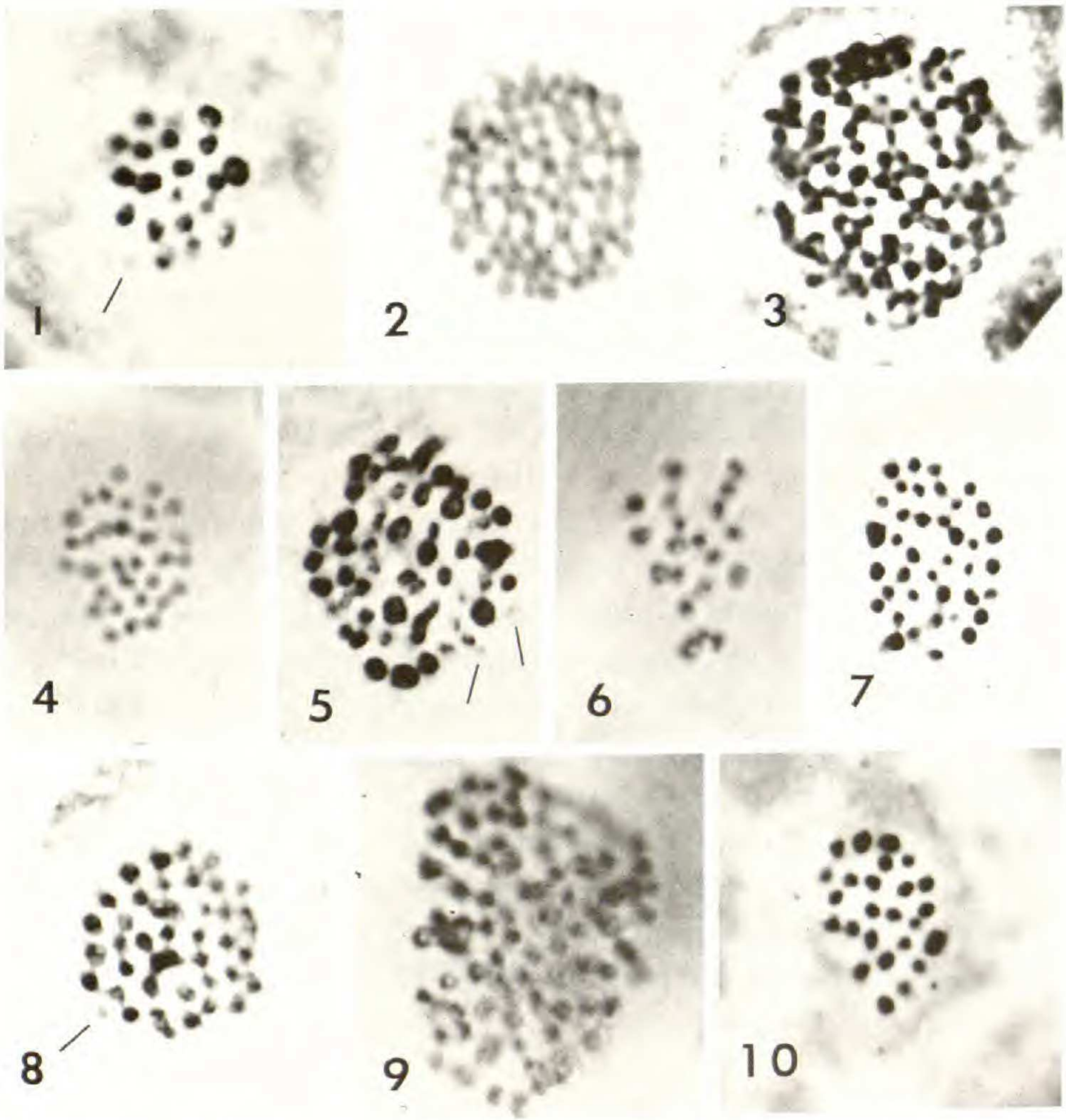
Most collections of both *Sedum ebracteatum* and *S. hemsleyanum* are polyploid, but 20 is clearly the basic number in both, and in this regard they differ from the other two species of the section. They are treated separately here, but the difficulty in assigning some plants definitely to one species or the other and the similarity in their basic chromosome numbers make a strong case for combining them.

A plant of *Sedum ebracteatum* from Hidalgo and another from cultivation both had $n = 20$ plus a small extra chromosome that commonly was unpaired (Figure 1), but eleven other collections originating from Durango (2), Jalisco (3), Guanajuato (2), San Luis Potosi (2), Queretaro (1), and Hidalgo (1) had $n = 40$ or minor variations from that. Three more had $n =$ ca. 80 (Figure 2), 14 others had $n =$ ca. 100, four more $n =$ ca. 120 (Figure 3), and the one from farthest north had $n =$ ca. 140. Most of the higher polyploids came from more easterly localities, in the Sierra Nevada Oriental, and those with $n = 40$ came from farther west. Nearly all of the higher polyploids were very irregular at meiosis, with univalents and multivalents at metaphase I and laggards and sometimes chromosome bridges at anaphase I. These irregularities also made exact counts of many of them not possible from meiosis, and chromosome numbers given for some of them are only approximations. Several may depart substantially from exact multiples of 20.

Meiotic irregularities of this sort generally lead to unbalanced dosages of chromosomes and genes in the reproductive cells and among the progeny. In diploids this imbalance commonly reduces fertility and survival, but high polyploids by definition have more copies of each gene, and unbalanced genotypes probably are less harmful to them than they are to diploids. Nevertheless, immediately after meiosis many microspore quartets in some polyploids have spores that differ in size, and later many of the immature pollen grains are undersized. These abnormalities indicate reduced fertility, but unfortunately little information is available regarding seed production and fertility in these collections, diploid or polyploid.

Sedum glabrum (Rose) Praeger

Sedum glabrum occurs on rocks on the dry western side of the northern Sierra Madre Oriental and on the adjacent plateau in the states of Coahuila, San Luis Potosi and western Nuevo Leon of northeastern Mexico. It is similar to *S. ebracteatum,* and Clau-



Figures 1–10. Chromosomes at first metaphase of meiosis, ×2000. (Univalents in three figures indicated by lines.) Figures **1–3**. *Sedum ebracteatum.* **1.** *M14743*, $n = 20 + 1B$. **2.** *C47-25*, $n = 80$. **3.** *U2789*, $n = 120$. Figures **4–5.** *S. glabrum.* **4.** *M7824*, $n = 31$. **5.** *U2104*, ca. 50 bivalents and multivalents + 2 univalents. Figures **6–9.** *S. hemsleyanum.* **6.** *UC57.173*, $n = 20$. **7.** *U2369*, $n = 40$. **8.** *U2359*, $n = 41 + 1$. **9.** *U1447*, $n =$ ca. 85. **10.** *S. hintonii*, *C47-72*, $n = 25$.

sen (1981) thought it possibly should be treated as a subspecies, but its leaves are generally thicker and slightly glaucous, flat above and completely glabrous, and it grows in a drier habitat. Cytologically it is very distinct: ten collections had $n = 31$ (Figure 4), and one was tetraploid with $n = 62$, and the cytological distinctness argues for maintaining it as a separate species.

One collection (*U2104*) listed here appears to be a hybrid with *Sedum ebracteatum.* It formed about 50 elements at metaphase I, including about 8–10 large, multilobed multivalents and several small univalents (Figure 5), and it had as many as five chromosome bridges at anaphase I.

Sedum hemsleyanum Rose

Sedum hemsleyanum, including *Sedastrum painteri* Rose (Clausen, 1959), has the most southerly distribution. It occurs mostly in the Sierra Madre del Sur and other southern mountains and more sparingly farther north into the trans-Mexican volcanic belt, where its distribution may slightly overlap that of *S. ebracteatum* (Clausen, 1959). A collection from Guatemala and another from Honduras both had larger leaves on the floral stems than the other collections, and both had $n = 20$ (Figure 6). However, 32 collections, mostly from the states of Puebla and Oaxaca, had $n = 40$ (Figure 7) or minor variations from that ($n = 41 + 1$ in Figure 8), and the species is primarily tetraploid. One collection from Oaxaca had $n = 60$, two from eastern Guerrero had $n =$ ca. 85 to 90 (Figure 9), one from Valle de Bravo, in the state of Mexico, had $n =$ ca. 97, another from Guerrero had $n =$ ca. 114 and one of unknown origin in the wild had $n =$ ca. 120. Most of the higher polyploids came from northerly localities for the species and possibly might more appropriately be assigned to the very similar *S. ebracteatum,* where high polyploids are common.

Sedum hintonii Clausen

Sedum hintonii is best distinguished by the dense covering of white hairs on all its stems, leaves and sepals. Described from a collection from western Michoacan, it is now known also from Jalisco and Durango (Clausen, 1981), but the three collections studied are all of unknown origin in the wild. All three have $n =$ 25 (Figure 10), and this species also is distinctive cytologically.

DISCUSSION

Morphologically the four species of Section Sedastrum appear to form a natural group, more similar to each other than any of them is to any other species. However, the three basic chromosome numbers, 20, 25, and 31, present a problem in understanding relationships. Many collections of *Sedum ebracteatum* and *S. hemsleyanum* from a broad geographic range do not have exact multiples of their apparent basic chromosome number of 20, but their cytological irregularities offer no real clues as to how the other basic numbers are related.

The significance of the meiotic irregularities that are so common in the high polyploids, especially in *Sedum ebracteatum,* also is unknown. Are the plants hybrids or apomicts, for example? Or is the meiotic irregularity tolerated because their high polyploidy buffers them against the consequences of unbalanced genotypes that would kill or sterilize a diploid? Information is needed regarding the sexual fertility of these plants in the wild.

LITERATURE CITED

BERGER, A. 1930. Crassulaceae. *In:* A. Engler, Ed., Die Natürlichen Pflanzenfamilien, 2nd ed. 18a: 352–485.

CLAUSEN, R. T. 1943. The section Sedastrum of *Sedum.* Bull. Torrey Bot. Club 70: 289–296.

———. 1959. *Sedum* of the Trans-Mexican volcanic Belt. Cornell Univ. Press, Ithaca, NY.

———. 1981. Variation of species of *Sedum* of the Mexican cordilleran plateau. Priv. pub., Ithaca, NY.

DECANDOLLE, A. P. 1828. Mem. Fam. Crassulaceae 37, Plate 6.

ROSE, J. N. 1905. North American Flora 22(1): 58.

UHL, C. H. 1976–1985. Chromosomes of Mexican *Sedum* I–V. Rhodora 78: 629–640; 80: 491–512; 82: 377–402; 85: 243–252; 87: 381–423.

PLANT BIOLOGY
CORNELL UNIVERSITY
ITHACA, NY 14853-5908

APPENDIX

Chromosome Numbers

Sedum ebracteatum DC

U2052 Durango. Near Tovar, 10 km W of Tepehuanes, ca. 2000 m. *M. Kimnach & F. K. Brandt 1192.* $n = 40$.

U2581 Durango. El Salto. *A. Lau 077.* $n = 40$.

C50-16 Tamaulipas. Canyon SW of Ciudad Victoria. J. L. Edwards. $n = 140–150$.

M6321 San Luis Potosi. Limestone cliff 2.4 km E of Santo Domingo, 1540 m. R. Moran. $n = 125 \pm 10$.

U2788 San Luis Potosi. 1.5 km SE of La Salitrera, 1970 m. *R. T. Clausen 77-41.* $n = 40$.

APPENDIX
Continued

M13367 San Luis Potosi. Bluff along Rio Santa Maria at E edge of Ocampo. R. Moran & C. H. Uhl. $n = 40 + 2$.
UC50.1060 Jalisco. Barranca near Atoyac, N of Guadalajara. Lefebure. $n = 40$ prob.
U2793 Jalisco. S slope, Barranca Oblatos, N of Guadalajara, 1500 m. *R. T. Clausen 77-24*. $n =$ ca. 40.
UC53.1156 Jalisco. Near Experiencia. *J. B. Zabaleta 17*. $n = 40 + 1$.
U2115 Guanajuato. Picachos de la Bufa, NE of Guanajuato city, 2350 m. $n = 40$.
M10194 Guanajuato. Km 32, near San Juan. R. Moran. $n =$ ca. 40.
C47-49 Guanajuato. Between Dolores Hidalgo and Guanajuato city. E. J. Alexander & C. L. Gilly. $n = 100$ prob.
M14766 Guanajuato. 16 km E of San Luis de la Paz. R. Moran. $n = 90–100$.
U1844 Guanajuato. 15.7 km E of San Jose Iturbide. $n = 90 \pm 10$.
U1859 Queretaro. 11 km W of Jalpan, 1070 m. $n =$ ca. 100.
U1851 Queretaro. 1.6 km N of Camargo. $n = 115–120$.
U1487 Queretaro. Cuesta China, 3 km E of Queretaro city, 1900 m. $n =$ ca. 100.
M7673 Queretaro. Nearby locality. R. Moran. $n =$ ca. 100.
M9888 Queretaro. Nearby locality. E. Gay. $n =$ ca. 120.
U2119 Queretaro. 12 km N of Cadereyta, 2200 m. $n = 40$.
U2789 Queretaro. Gorge of San Juan River, 2.5 km S of San Juan del Rio, 1940 m. *R. T. Clausen 80-27*. $n = 120$ (Figure 3).
U1874 Hidalgo. Mex. 85, 16 km NE of Zimapan. $n = 100 \pm 2$.
M14743 Hidalgo. N of Tecozautla, 1650 m. R. Moran. $n = 20 + 1B$ (Figure 1).
M14749 Hidalgo Geysers, Tecozautla, 1550 m. R. Moran. $n = 40$.
U1542 Hidalgo. 1.6 km E of Chilcuautla. $n = 80$.
M6415 Hidalgo. Canon Venados. G. Lindsay. $n =$ ca. 100.
M7790 Hidalgo. El Carmen. R. Moran. $n =$ ca. 100.
U1472 Hidalgo. Topotype of *Sedastrum pachucense* Thompson. Hwy. 105, 0.5 km NE of Pachuca city limits. $n =$ ca. 100.
U1547 Hidalgo. 2.4 km S of Epazoyucan. $n = 100 \pm 10$.
U1411 Michoacan. Puente Rio Turundeo, 8.4 km N of Tuxpan on Mex. 15, 1830 m. $n = 118 \pm 3$.
U1442 Guerrero. Zopilote Canyon, 18.5 km N of Chilpancingo. $n = 105-110$.
C47-34 Cultivated. F. Schmoll. $n = 20 + 1$.
C47-29 Cultivated. F. Schmoll. $n = 40 + 1$.
C47-25 (Figure 2), *C47-28* Both cultivated, F. Schmoll. $n = 80 \pm 1$.
C43-25 Cultivated. R. T. Clausen. $n = 105 \pm 2$.
C47-84 Cultivated. *E. K Balls 4949*. $n =$ ca. 100.

Sedum glabrum (Rose) Praeger
U2769 Coahuila. Ridge N of San Miguel, 22 km NW of Saltillo, 1300 m. *R. T. Clausen 80-7*. $n = 31$.

APPENDIX
Continued

U1521B Coahuila. Ridge W of Mex. 57, 18 km N of Saltillo. $n = 31$.
M7824 Coahuila. Chorro Canyon, ESE of Saltillo. R. Moran. $n = 31$ (Figure 4).
U2403 Nuevo Leon. Top of cable lift, Grutas de Garcia. J. Bauml. $n = 31$.
U2402 Nuevo Leon. Huasteca Canyon. M. Flores. $n = 31$.
U1493 San Luis Potosi. Hill W of Mex. 57, 8.5 km S of Nunez. $n = 62$.
U2104 San Luis Potosi. Rocks E of Mex. 57, 1 km S of San Lorenzo. (Probable hybrid with *S. ebracteatum*.) Ca. 50 elements (Figure 5).
U2730 San Luis Potosi. 1 km S of La Zapatilla. *R. T. Clausen 80-26*. $n = 31$.
U1492 San Luis Potosi. Bluff E of Mex. 57, 1.1 km S of bridge over Rio Santa Maria. $n = 31$.
UC49.1978 Cultivated. *James West 743*. $n = 31$.
M3280, UC52.1768 Both cultivated. $n = 31$.

Sedum hemsleyanum Rose
U1424 Edo. Mexico. W side of lake at Valle de Bravo, 1800 m. $n =$ ca. 97.
C47-47, C47-48 Edo. Mexico. Barranca de Texolotengo, 6 km S of Villa Guerrero. *Gilly, Alexander* & *Xolocotzi 126* & *133*. Both $n = 40$.
U1428 Edo. Mexico. N side, Puente de Calderon, Mex 55, 12.2 km S of Villa Guerrero. $n = 40$.
U1464 Morelos. Probable topotype of *Sedastrum painteri* Rose. El Salto de San Anton, W of Cuernavaca. N. W. Uhl. $n = 40$.
U1290 Morelos. 9 km from Cuernavaca on road to Tepoztlan. *M. Kimnach K374*. $n = 40$.
U2355 Puebla. 4.3 km E of Aquixtla, 2050 m. $n = 41$.
U1449 Puebla. Canyon 1.5 km E of Tepenco. $n = 40$.
U1450 Puebla. 2.4 km SE of El Tepenene. $n = 40$.
U1451 Puebla. Bluff 17.3 km SW of Acatlan, 1300 m. $n = 40$.
U1655 Puebla. Nearby locality. *W. Handlos 407A*. $n = 40$.
M6399 Puebla. River cliffs near Petlalcingo, 1325 m. R. Moran. $n = 40$.
U2359 Puebla. 6.4 km N of Penafiel. $n = 41 + 1$ (Figure 8).
M6359 Puebla. San Antonio Texcala, near Tehuacan. R. Moran. $n = 39 + 1$.
M6360 Puebla. Nearby locality. R. Moran. $n = 40$.
OM4 Veracruz. W of Maltrata. R. T. Clausen. $n = 40 + 2$.
U1888 Veracruz. S side of Rio Blanco, opposite city. $n = 40$.
O-RB2 Veracruz. Nearby locality. R. T. Clausen. $n = 39$–40.
C47-102 Guerrero. 25 km W of Iguala on road to Teloloapan. L. F. Randolph. $n = 114 \pm 2$.
U1447 Guerrero. 11 km NE of Taxco. $n = 85 \pm 3$ (Figure 9).
M10169 Guerrero. Canon del Mano, near Iguala. R. Moran $n = 40$.
U1440 Guerrero. 8.5 km E of Chilpancingo. $n =$ ca. 90.
M6366 Oaxaca. 6 km N of Miltepec, 2050 m. R. Moran. $n = 40$.
U1453 Oaxaca. 2.5 km S of Camotlan. $n = 40$.
U2866 Oaxaca. 14 km NE of Teotitlan del Camino, 1525 m. $n = 40$.
U2658 Oaxaca. Nearby locality. *J. Bauml* & *M. Kimnach 392*. $n = 40$.
U2411 Oaxaca. 11 km NW of Yanhuitlan. $n = 40$.

APPENDIX
Continued

U2092 Oaxaca. Nearby locality. *W. Handlos 542A.* $n = 40$.
U2095 Oaxaca. Ca. 19 km NE of Yolomecatl. *W. Handlos 552B.* $n = 40$.
U2319 Oaxaca. Near Tlaxiaco, 1980 m. *F. Boutin 3941.* $n = 40 + 1$.
U2306 Oaxaca. Ixtlan. T. MacDougall. $n = 40$.
M7777 Oaxaca. San Hipolito. R. Moran. $n = 40$.
C47-50 Oaxaca. Sierra de San Felipe. A. J. Sharp. $n = 40$.
U2369 Oaxaca. Ca. 5 km E of Oaxaca city, 1800 m. $n = 40$ (Figure 7).
U1650 Oaxaca. 18 km of Totolapan. *W. Handlos 331A.* $n = 40$.
U1353 Oaxaca. Rio de Lapaguia, Miahuatlan. *T. MacDougall B-251.* $n = 60$.
UC57.246 Guatemala: Dept. Sacatepequez. Epiphytic near Alotenango, 1350 m. C. K. Horich. $n = 20$.
UC57.173 Honduras: Dept. Francisco Morazan. E slope of Cerro Berrinche. C. K. Horich. $n = 20$ (Figure 6).
C-47-3 Cultivated. Schmoll. $n = 120 \pm 2$.
C47-87 Cultivated. T. MacDougall. $n = 40$.

Sedum hintonii Clausen
U1746 Cultivated. J. Marnier-Lapostolle. $n = 25$.
U2689 Cultivated. Univ. of Guadalajara. $n = 25$.
C47-72 Cultivated. F. Schmoll. $n = 25$ (Figure 10).